

Fish or jellies—a question of visibility?

Abstract—Light is an important limiting factor for the visual foraging process in fishes, and the light regime may potentially affect the competition between visual and tactile predators. We investigated two equal-sized fjords of quite different pelagic food web structure. Earlier studies have revealed that the jellyfish *Periphylla periphylla* dominates Lurefjorden, while fish predators dominate in the other fjord, Masfjorden. Furthermore, the mesozooplankton stock of Lurefjorden is larger in both total biomass and size of the individuals. Hence, earlier hypotheses linking the competitive advantage of tactile gelatinous plankton predators to smaller-sized mesozooplankton communities are unable to explain the present phenomenon. To see if the difference in the pelagic biota of the two fjords could be associated with characteristics of the light regime, we measured the light absorbance in the basin water of the two fjords. We found that, due to a slightly stronger influence of coastal water in the basin water of Lurefjorden, the exponential light absorbance coefficient below 100 m is two to three times higher there than in other fjords. This results in a reduction in light flux of several orders of magnitude, effectively reducing the possibility of visual foraging. The tactile mode of predation in jellyfish, however, is not influenced, and we hypothesize that the visibility regime has a decisive role in structuring the pelagic food webs of the two fjords.

The question why some pelagic ecosystems support large stocks of fish while others are dominated by jellyfish has received much attention in marine ecology. Mills (1995) points out that as world fisheries begin to experience serious

declines, it is relevant to recognize that the carnivorous jellyfishes are ubiquitous and are thus opportunistically positioned to utilize secondary production that is ordinarily consumed by fish. It has been hypothesized that while fish forage most efficiently on large forms of zooplankton (Brooks and Dodson 1965), they may be out-competed by jellyfish if the prey stock is dominated by small size classes (Greve and Parsons 1977), and that fish recruitment can fail, due to prey depletion by large standing stocks of jellyfish (Möller 1980). Here we show that neither of these hypotheses are likely to account for pelagic food web differences observed among fjords. Instead we argue for an alternative hypothesis recently worked out in theory (Eiane et al. 1997): that poor visibility in the water column may prevent the visually foraging planktivorous fishes from obtaining the foraging rates required for population maintenance while tactile planktivores, such as jellyfish, are not affected.

Light limitation in visual foraging—The present work and the study of Eiane et al. (1997) emerged as a result of theoretical and experimental work on how predation by fish is affected by light and optical properties of prey and environment (Aksnes and Giske 1993; Giske et al. 1994; Aksnes and Utne 1997; Utne 1997). Furthermore, field studies on the mesopelagic fish *Maurollicus muelleri*, an important zooplanktivore in Norwegian fjords, have revealed that both the feeding and the vertical behavior are highly sensitive to the prevailing light conditions of the water column (Giske and

Aksnes 1992; Baliño and Aksnes 1993; Rosland and Giske 1994, 1997). According to the model derived by Aksnes and Giske (1993) and Aksnes and Utne (1997), visual feeding rate (f) can be expressed

$$f = \frac{h^{-1}N}{[h\pi(r \sin \theta)^2\nu]^{-1} + N}, \quad (1)$$

where h is handling time, N is prey abundance, ν is cruising speed of the predator (turbulence and prey motility, however, will also enter this parameter, see Fiksen et al. 1998), θ is the reaction half angle, and r is the visual range of the predator. Sensitivity analyses (Aksnes and Giske 1993; Eiane et al. 1997; Fiksen et al. 1998) clearly indicate the high sensitivity of feeding rate to the visual range parameter. According to Aksnes and Utne (1997), the visual range (r) of Eq. 1 is expressed as

$$r^2 e^{cr} = |C_o| A_p E' \frac{E_b}{K_e + E_b}, \quad (2)$$

where c is beam attenuation, C_o is inherent contrast of prey, A_p is prey size (measured as area), E_b is background irradiance at the depth z , and E' and K_e are parameters indicating the sensitivity of the visual system of the predator. The background irradiance (at large depths) can be approximated by Beers law:

$$E_b = E_0 e^{-kz}, \quad (3)$$

where E_0 is surface irradiance, z is depth, and k is the attenuation coefficient for diffuse light. According to the analysis of Eiane et al. (1997), the competition between visual and tactile predators of a water column is strongly influenced by parameters concerning the optical regime and in particular by k (Eq. 3). Hence, from theory it is expected that large water columns with high light extinction reduce the visual foraging possibilities (as in most fishes). However, there are no reasons that the tactile mode of predation (as in most jellyfish) should be influenced.

Lurefjorden and Masfjorden; a jellyfish fjord and a fish fjord—In this study, we focus on two fjord systems. Masfjorden can be characterized as a fish fjord that is representative of most western Norwegian fjords in that the dominating zooplankton predators are the mesopelagic fishes *M. muelleri* and *Benthosema glaciale*. The pelagic biota of this fjord is well known and has been studied in a number of papers (Kaaertvedt et al. 1988; Giske et al. 1990; Salvanes et al. 1995 and references therein). In the nearby Lurefjorden, mesopelagic fishes are absent, but instead the fjord presently houses a large population of the jellyfish *Periphylla periphylla*.

Lurefjorden and Masfjorden are comparable with respect to maximum depth (495 m in Masfjorden versus 440 m in Lurefjorden) and surface area (25 versus 30 km²). Furthermore, they are located less than 20 km apart from each other and connect top open waters through a common coastal entrance. The sill depths of the two fjords, which are 20 and 70 m for Lurefjorden and Masfjorden, respectively, represent the main topographic difference. As shown later, a consequence of this is that the basin water of Lurefjorden is slight-

ly more influenced by coastal water than the basin water of Masfjorden.

The first scientific report on the high *P. periphylla* abundance in Lurefjorden was made by Johannessen (1980) reporting a catch of about 500 kg wet weight taken during half an hour with a small trawl. According to Fosså (1992), local fishermen have observed *P. periphylla* in varying amounts at least from the late 1940s, but in the early 1970s, a population explosion apparently took place because medusae began clogging fishing nets. From that time on, the nuisance has become worse (Fosså 1992).

According to Fosså (1992), the *P. periphylla* abundance of Lurefjorden corresponds to about 6 g ash-free dry weight m⁻² or 18 g dry weight m⁻² (integrated over the depth range 0–360 m). Calculations indicate that the total population size is above 10⁴ tonnes wet weight, which is extremely high considering the small geographical scale of Lurefjorden (30 km²). According to Fosså (1992) and our own unpublished observations, a 10-min trawl haul in Lurefjorden may yield several tonnes of *P. periphylla*. The peculiar pelagic biota of Lurefjorden is characterized by its echogram (Fig. 1). Compared to other fjords, almost no fish scatter can be detected in Lurefjorden. In addition to a high *P. periphylla* stock, the biomass estimates given by Salvanes et al. (1995) indicate a high mesozooplankton stock and no mesopelagic fish in Lurefjorden, while Masfjorden shows the opposite pattern (Table 1). Nesse (1994) also observed that the larger copepods, such as *Calanus* sp. and *Euchaeta norvegica*, were four to eight times more abundant in Lurefjorden than in Masfjorden.

Are fish limited by light in Lurefjorden?—Based on our knowledge of the very different pelagic biota of the two fjord systems, we arranged cruises in October 1995 and in January 1996. In order to test whether differences in the light regime of Masfjorden and Lurefjorden might account for the different predator regimes of the two fjords (according to Eiane et al. 1997), light absorbance was measured with a Shimadzu UV-160 spectrophotometer during the two cruises. Measurements were made on water samples obtained throughout the water column. In addition to Masfjorden and Lurefjorden, light absorbance measurements were also made in Sognefjorden and Osterfjorden.

Below approximately 100 m depth, we found that the absorbance of light in Lurefjorden was consistently higher than for Masfjorden (Fig. 2). At 200 m depth, being representative for the basin waters of Lurefjorden, Masfjorden, Sognefjorden, and Osterfjorden, the light absorbance of Lurefjorden was two to three times higher than in the other fjords (Fig. 3). The attenuation coefficient of the downward-directed light flux is normally largely determined by absorbance (Sathyendranath and Platt 1990), suggesting an attenuation coefficient (k , see Eq. 3) about twice as high in Lurefjorden as in the other fjords.

The daytime depth distribution of *M. muelleri* in Masfjorden in winter has been shown to track the 6×10^{-3} $\mu\text{mol m}^{-2} \text{s}^{-1}$ isolume (at about 150 m depth at noon) (Baliño and Aksnes 1993). This corresponds to the lowest light level at which feeding is observed in *Pagothenia borchgrevinki*, the only planktivorous fish commonly found beneath the annual

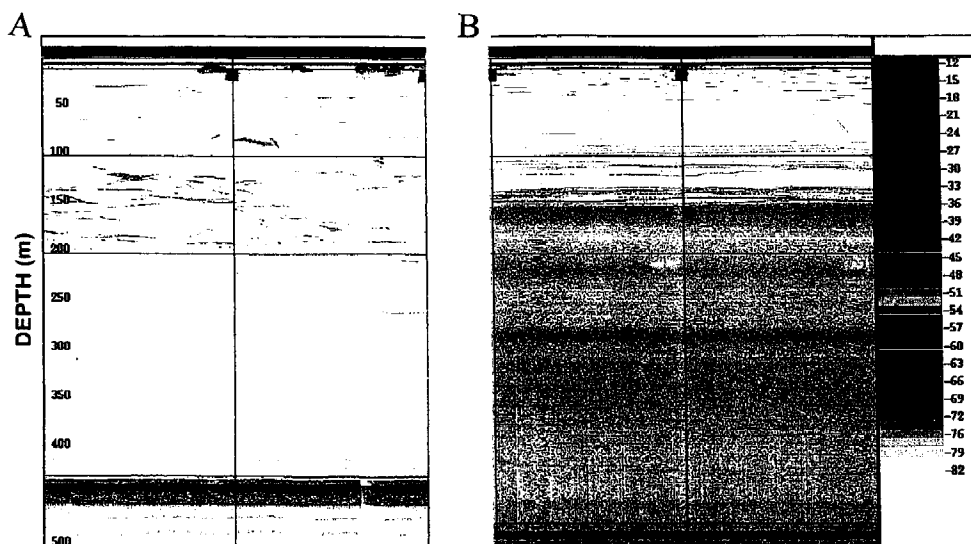


Fig. 1. Echograms (38 kHz) from (A) Lurefjorden at 10:47–11:02 (GMT) on 9 January 1996, and (B) Masfjorden at 10:40–10:55 on 7 January 1996. In Masfjorden trawling has shown that the upper pronounced sound-scattering layer (130–170 m) is dominated by the mesopelagic fish *M. muelleri*. The layers below 200 m consist mainly of the mesopelagic fish, *B. glaciale*, some krill (*M. norvegica*), prawns (*Sergestes arcticus* and *Pasiphaea multidentata*), and blue whiting (*Micro-mesistius poutassou*). In Lurefjorden trawling has given catches totally dominated by *P. periphylla*, although some krill (*M. norvegica*) and some whiting (*Merlangius merlangus*) are encountered. Color code refers to volume backscattering strength (dB).

sea-ice in Antarctica (Montgomery et al. 1989). Twice the attenuation of downward light flux in Lurefjorden compared with other fjords (Figs. 2, 3) implies (Eq. 3) that the light flux in the basin waters will be several orders of magnitude lower in Lurefjorden, suggesting a severe reduction in the potential for visual feeding (Giske and Aksnes 1992; Aksnes and Giske 1993; Aksnes and Utne 1997). The importance of light flux and water optics for predator–prey relations has been well documented experimentally (Vinyard and O'Brien 1976; Wright and O'Brien 1984; Montgomery et al. 1989; Gregory and Northcote 1993; Thetmeyer and Kils 1995; Utne 1997) and in the field (Kaartvedt 1996; Kaartvedt et al. 1996). Hence, we cannot reject the hypothesis that a much higher light absorbance in the basin water of Lurefjorden (Figs. 2, 3) effectively reduces the possibility of visual predation at depths where suitably-sized prey is abundant.

Why does the basin water of Lurefjorden have a higher light absorbance than the other fjords, and has this difference always been present? The answer to the first of these ques-

tions seems straightforward. The shallow sill (20 m) of Lurefjorden prevents intrusion of dense, deep water (see Fosså [1992] and references therein). Thus, the basin water of Lurefjorden is largely of coastal origin (salinity below 34.5‰) while the basin water of Masfjorden, Osterfjorden, and Sognefjorden, as well as most other fjords on the western coast of Norway, typically is Norwegian trench water (salinity above 34.5‰) (Gade and Edwards 1980). Therefore, the basin water in Lurefjorden is slightly colder and less saline

Table 1. Biomass (mg C m⁻³) of zooplankton, mesopelagic fish (*M. muelleri* and *B. glaciale*), and *P. periphylla* (modified from Salvanes et al. 1995).

	Zooplankton		Mesopelagic fish		<i>P. periphylla</i>	
	Autumn	Spring	Au-	Spring	Autumn	Spring
			tumn			
Masfjorden	3.92	2.66	1.32	2.63	0.00	0.00
Lurefjorden	31.60	7.92	0.00	0.00	10.4	26.4

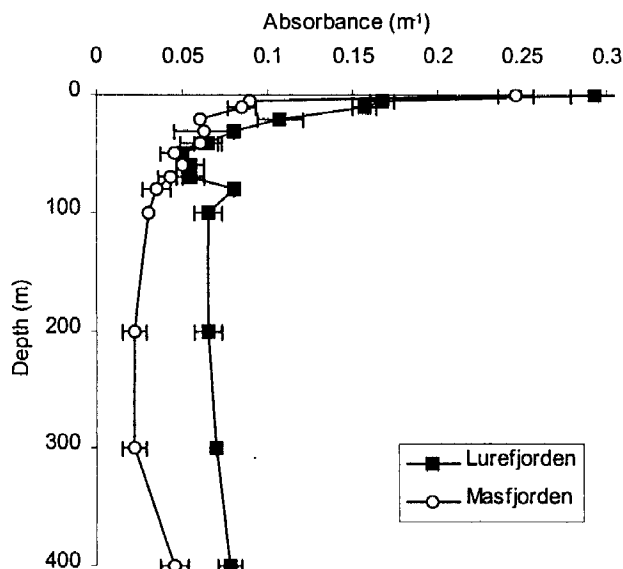


Fig. 2. Light absorbance (450 nm) in Lurefjorden and Masfjorden in October 1995. Bars denote 95% confidence limits.

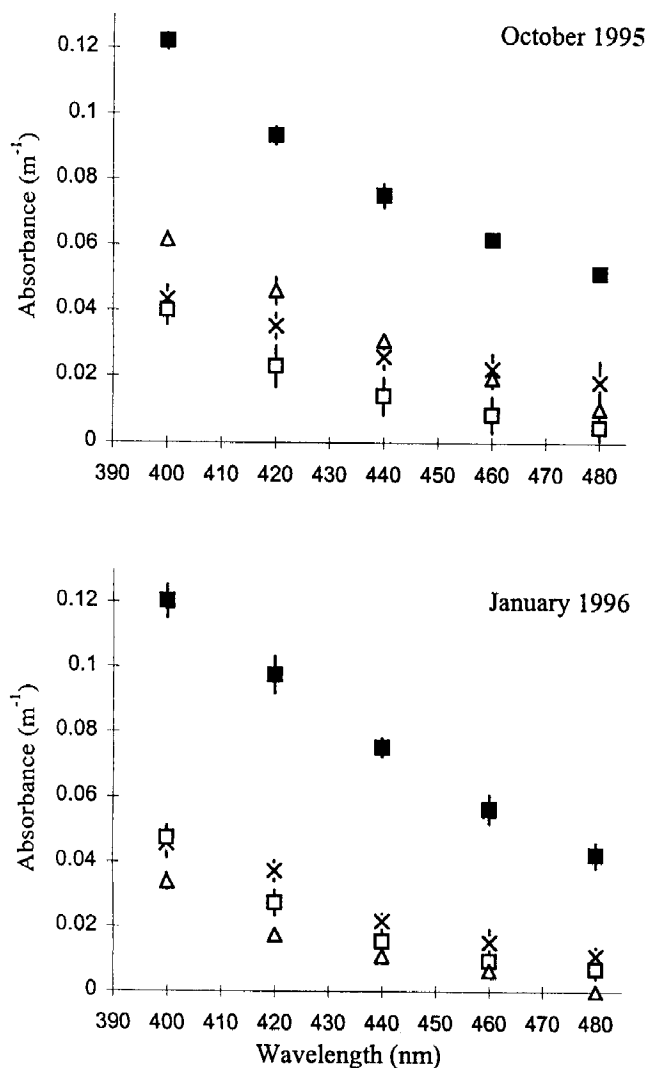


Fig. 3. Light absorbance in the basin waters of four fjords in October 1995 and January 1996 measured at 400, 420, 440, 460, and 480 nm. Open squares are from Masfjorden, closed squares are from Lurefjorden, open triangles are from Osterfjorden, and \times s are from Sognefjorden. Bars denote 99% confidence intervals. Absence of significant visual predation pressure seems to give rise to an exceptional high stock of mesozooplankton (especially the relatively larger ones) that represent a good food source for tactile predators like *P. periphylla*.

than in Masfjorden (6.5°C versus 7.6°C and 33.1‰ versus 34.9‰ measured at 200 m depth in our study). The mixing diagram (Fig. 4) clearly demonstrates that the higher light absorbance in the deep water of Lurefjorden is attributed to the higher proportion of coastal water. This is plausible because it is well known that light extinction of freshwater-influenced coastal waters is higher than the more saline water masses located below. The second question, whether the light absorbance of Lurefjorden has always been high, is more difficult to answer as no historical data exist. From the mixing diagram (Fig. 4) and the above analysis, it can be concluded that regional rather than local processes determine the light absorbance of the basin water of Lurefjorden. The

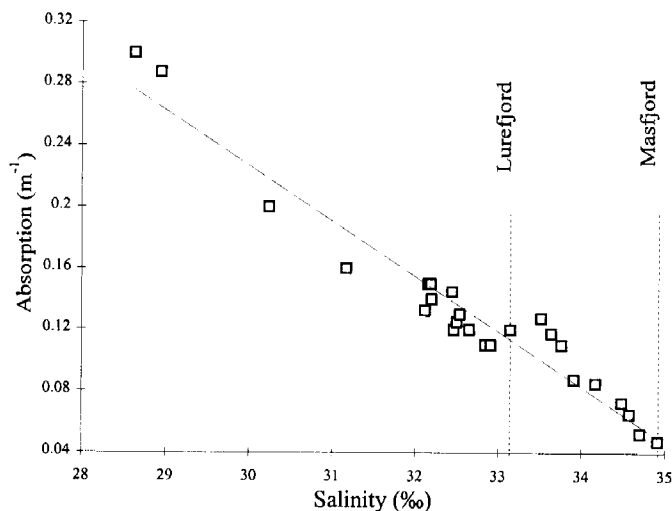


Fig. 4. Mean absorbance (at 400 nm) plotted against salinity sampled at different depths in Lurefjorden and Masfjorden, in winter 1995/1996, indicating a strong relationship between absorbance and the component of low salinity coastal water. The line of best fit is indicated ($Y = -0.036X + 1.3076$; $R^2 = 0.94$) together with values from the basin water (at 200 m) of Masfjorden and Lurefjorden.

freshwater component of the coastal waters off the Norwegian coast originates from the Baltic Sea and the rivers entering the North Sea. Thus, it may be speculated that the light absorbance of the basin water of Lurefjorden has been affected by regional eutrophication processes and may relate to the increase in *P. periphylla* since the 1970s. However, climatic variability, through its influence on basin water exchanges may also affect the proportion of coastal water in the basin water of Lurefjorden, thereby affecting the light absorbance properties of the basin water of Lurefjorden on a decadal time scale.

The light absorbance of Sognefjorden and Sørfjorden was similar to that of Masfjorden (Fig. 3). The pelagic biota of Sognefjorden and Osterfjorden is less documented than in Masfjorden and Lurefjorden. Salvanes et al. (1995) found that the abundance of mesopelagic fishes in Osterfjorden was comparable to that of Masfjorden. Mesopelagic fishes are also abundant in Sognefjorden (Bagøien et al. in prep.). Fosså (1992) showed that all the above-mentioned fjords, as well as offshore waters of Norway in general, contain *P. periphylla*. Based on what is known to date (Fosså 1992; Bagøien et al. in prep.), the abundance of the Sognefjorden population is several orders of magnitude below the population in Lurefjorden, but *P. periphylla* is more frequent in Sognefjorden than in Masfjorden and Osterfjorden. This may indicate mechanisms, other than light-associated factors, governing success of *P. periphylla*. However, Sognefjorden is the deepest fjord of the Norwegian coast (maximal depth of 1,308 m compared to 495 and 620 m depth of Masfjorden and Osterfjorden, respectively). As hypothesized for Lurefjorden, one effect of this that a large part of the Sognefjorden water column presumably not will be very favorable for visual predation. According to Fosså (1992) most *P. peri-*

phylla in Sognefjorden were found below 350 m (i.e., deeper than in Lurefjorden).

Other hypotheses—Earlier observations have shown that the zooplankton stock of Lurefjorden is higher than in Masfjorden (see Table 1). On the cruises in 1995 and 1996, we also measured the size distribution of the dominant prey item *Calanus* spp. in order to see if differences at this level can explain (according to Brooks and Dodson 1965; Greve and Parsons 1977) the dominance of jellyfish in Lurefjorden. Zooplankton samples were obtained with a Multinet (Hydrobios) equipped with 180- μ m mesh size. According to recent unpublished molecular genetical studies, *Calanus finmarchicus*, *Calanus helgolandicus*, and *Calanus glacialis* may be present in Norwegian coastal waters. Based on the cruises in October 1995 and January 1996, we found that Lurefjorden sustained a significantly higher mesozooplankton biomass (average wet weight $g\ m^{-2} \pm SE = 76.6 \pm 3.0$; $n = 5$) than Masfjorden (14.8 ± 1.6 ; $n = 5$). This is in accordance with previous studies (Nesse 1994; Salvanes et al. 1995). Additional to the observation of Nesse (1994), that the larger copepods were much more abundant in Lurefjorden, we observed that stage V copepodites *Calanus* spp. (the numerically and biomass dominant component of the mesozooplankton) in Lurefjorden were significantly larger (average cephalothorax length $\pm SE = 2.545 \pm 0.011$ mm; $n = 450$) than in Masfjorden (2.250 ± 0.008 mm; $n = 343$). The smaller size of the dominant zooplankton in Masfjorden is in accordance with the contention that visual predators exert a selective pressure against large individuals (Brooks and Dodson 1965). In Lurefjorden, however, visual predators seem to fail to establish in spite of high abundance of appropriate prey organisms, rejecting a causal relationship with zooplankton composition (Greve and Parsons 1977; Möller 1980).

The high abundance of *P. periphylla* might conceivably contribute to making Lurefjorden an inferior environment for mesopelagic fish. Predation on herring larvae by large stocks of *Aurelia aurita* has been suggested as a mechanism controlling the recruitment of herring in the Baltic Sea (Möller 1984). Available data suggest that crustaceans are the dominating prey of *P. periphylla* (Fosså 1992; Eiane in prep.), but predation upon fish can, of course, not be ruled out. The distribution of the mesopelagic fishes *B. glaciale* and *M. muelleri* overlaps the distribution of *P. periphylla* throughout most of Norwegian waters (Fosså 1992), indicating that coexistence is common. Although possible, we consider it unlikely that mesopelagic fish are excluded by *P. periphylla* predation in Lurefjorden and not elsewhere.

In 1922 the Danish biologist Knudsen (1922) wrote: "In studying those properties of water, and particularly of sea water, which are of importance to the organisms living therein, a study of the light-contents of the water must occupy a prominent place." Since then, the light flux and optical properties of the water column have become main topics in the study of primary production in aquatic ecosystems. However, light flux and water optics is rarely considered in ecological studies concerning dynamics of higher trophic levels. In the Black Sea, for instance, eutrophication has reduced visibility by a factor of two to three, yet no relation has been

made to the concurrent decline in fish abundance and explosive growth in gelatinous zooplankton populations (Zaitsev 1992).

The present study gives some support to the hypothesis that the visibility regime may affect the distribution of tactile and visual predators such as jellyfish and fish (Eiane et al. 1997). We believe this has implications deserving attention in the study of light as forcing for marine ecosystem dynamics through the visual feeding process (Eqs. 1–3) and more specifically in studies of potential effects of eutrophication. Of course, our study does not prove a mechanistic relationship between the higher absorbance in Lurefjorden and the reduced amount of fish in this fjord relative to Masfjorden. Stronger evidence is obviously needed, and comparative studies of the food web structure of fjords with different visibility regimes will be valuable in further studies addressing the question: Fish or jellies—a question of visibility?

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References

- AKSNES, D. L., AND J. GISKE. 1993. A theoretical model of aquatic visual feeding. *Ecol. Modell.* **67**: 233–250.
- , AND A. C. W. UTNE. 1997. A revised model of visual range in fish. *Sarsia* **82**: 137–147.
- BALIÑO, B. M., AND D. L. AKSNES. 1993. Winter distribution and migration of the sound scattering layers, zooplankton and micronecton in Masfjorden, western Norway. *Mar. Ecol. Prog. Ser.* **102**: 35–50.
- BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size, and composition of plankton. *Science* **150**: 28–30.
- EIANE, K., D. L. AKSNES, AND J. GISKE. 1997. The significance of optical properties in competition among visual and tactile planktivores: A theoretical study. *Ecol. Modell.* **98**: 123–136.
- FIKSEN, Ø., A. C. W. UTNE, D. L. AKSNES, K. EIANE, J. V. HELLEVIK, AND S. SUNDBY. 1998. Modelling the influence of light, turbulence and ontogeny on ingestion rates in larval cod and herring. *Fish. Oceanogr.* **7**: 355–363.
- FOSSÅ, J. H. 1992. Mass occurrence of *Periphylla periphylla* (Scyphozoa, Coronatae) in a Norwegian fjord. *Sarsia* **77**: 237–251.

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- GADE, H. G., AND A. EDWARDS. 1980. Deep water renewal in fjords, p. 453-489. In H. J. Freeland, D. M. Farmer, and C. D. Levings [eds.], *Fjord oceanography*. Plenum.
- GISKE, J., AND D. L. AKSNES. 1992. Ontogeny, season and trade-offs: Vertical distribution of the mesopelagic fish *Maurolicus muelleri*. *Sarsia* **77**: 253-261.
- , ———, AND Ø. FIKSEN. 1994. Visual predators, environmental variables and zooplankton mortality risk. *Vie and Milieu* **44**: 1-9.
- , AND OTHERS. 1990. Vertical distribution and trophic interactions of zooplankton and fish in Masfjorden, Norway. *Sarsia* **75**: 65-81.
- GREGORY, R. S., AND T. G. NORTHCOTE. 1993. Surface, planktonic, and benthic foraging by juvenile chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. *Can. J. Fish. Aquat. Sci.* **50**: 233-240.
- GREVE, W., AND T. R. PARSONS. 1977. Photosynthesis and fish production: Hypothetical effects of climatic change. *Helgol. Wiss. Meeresunters.* **30**: 666-672.
- JOHANNESSEN, P. 1980. Resipientundersøkelser av enkelte fjordavsnitt i Lindås kommune med hovedvekt lagt på bunnforhold og bunndyr. Report from Department of Marine Biology, Univ. of Bergen.
- KAARTVEDT, S. 1996. Habitat preference during overwintering and timing of seasonal vertical migration of *Calanus finmarchicus*. *Ophelia* **44**: 145-156.
- , D. L. AKSNES, AND A. AADNESEN. 1988. Winter distribution of macroplankton and micronekton in Masfjorden, western Norway. *Mar. Ecol. Prog. Ser.* **45**: 45-55.
- , W. MELLE, T. KNUITSEN, AND H. R. SKJOLDAL. 1996. Vertical distribution of fish and krill beneath water of varying optical properties. *Mar. Ecol. Prog. Ser.* **136**: 51-58.
- KNUDSEN, M. 1922. On measurement of the penetration of light into the sea. *Publ. Circnst. Cons. Perm. Int. Explor. Mer* **76**.
- MILLS, C. E. 1995. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. *ICES J. Mar. Sci.* **52**: 575-581.
- MONTGOMERY, J. C., N. W. PANKHURST, AND B. A. FOSTER. 1989. Limitations on visual food-location in the planktivorous Arctic fish *Pagothenia borchgrevinki*. *Experimentia* **45**: 395-397.
- MÖLLER, H. 1980. Scyphomedusae as predators and food competitors of larval fish. *Meeresforsch. Rep. Mar. Res.* **28**: 90-100.
- . 1984. Reduction of a larval herring population by a jellyfish predator. *Science* **224**: 621-622.
- NESSE, T. B. 1994. En sammenligning av zooplanktonsamfunnet i Lurefjorden og Masfjorden, og mulig innflytelse av *Periphylla periphylla*. Unpubl. thesis for the cand. scient. degree. Univ. of Bergen, Bergen.
- ROSLAND, R., AND J. GISKE. 1994. A dynamic optimization model of the diel vertical distribution of a pelagic planktivorous fish. *Prog. Oceanogr.* **34**: 1-43.
- , AND ———. 1997. A dynamic model for the life history of *Maurolicus muelleri*, a planktivore fish. *Fish. Oceanogr.* **6**: 19-34.
- SALVANES, A. G. V., D. L. AKSNES, J. H. FOSSÅ, AND J. GISKE. 1995. Simulated carrying capacities of fish in Norwegian fjords. *Fish. Oceanogr.* **4**: 17-32.
- SATHYENDRANATH, S., AND T. PLATT. 1990. The light field in the ocean: Its modification and exploitation by the pelagic biota, p. 3-18. In P. J. Herring, A. K. Campbell, M. Whitfield, and L. Maddock [eds.], *Light and life in the sea*. Cambridge Univ. Press.
- THETMEYER, H., AND U. KILS. 1995. To see and not be seen: The visibility of predator and prey with respect to feeding behaviour. *Mar. Ecol. Prog. Ser.* **126**: 1-8.
- UTNE, A. C. W. 1997. The effect of turbidity and illumination on the reaction distance and search time of the marine planktivore *Gobiusculus flavescens*. *J. Fish Biol.* **50**: 926-938.
- VINYARD, G. L., AND W. J. O'BRIEN. 1976. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). *J. Fish. Res. Bd. Can.* **33**: 2845-2849.
- WRIGHT, D. I., AND W. J. O'BRIEN. 1984. The development and field test of a tactical model of the planktivorous feeding of white crappie (*Pomoxis annularis*). *Ecol. Monogr.* **54**: 65-98.
- ZAITSEV, Y. P. 1992. Recent changes in the trophic structure of the Black Sea. *Fish. Oceanogr.* **1**: 180-189.

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